An Essay on the Development of the Mouth Parts of Certain Insects.

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Since the publication of my paper on the mouth parts of the *Diptera*, printed in the *Transactions* of the American Entomological Society for 1894, I have continued gathering material, have examined the oral parts of a very large number of species of all orders, and am more than ever convinced that in all essentials the conclusions already published by me are correct—revolutionary as they seem at first sight. That my ideas have not found unquestioned acceptance is not surprising; but no one has, to my knowledge, published anything that disproves the points made by me. It has been suggested, however, because I have not made continual reference to the works of previous authors, that I was ignorant of the literature, and several papers have been cited as contradicting my conclusions.

As a matter of fact I believe I am fully aware of all that has been written on the subject, and have, in each case where my attention has been called to a paper, studied it carefully, and found nearly always that the facts given bear me out, though the conclusions are adverse: simply because no author has seriously questioned the universally accepted homology of the mouth parts in the various orders. My own studies have been made on a basis so radically different from any heretofore accepted, that my results must stand on them alone, and my conclusions, if valid, must stand on the facts as they appear to me. I have used principally the dissecting needles in my work; but have not neglected the section cutter. This latter instrument has been rather too much used at the expense of the needles, and its results, though undoubtedly accurate as a record of facts, are easily misinterpreted if the basic homology which is assumed

to exist is inaccurate. For the reasons just given no references to previous writers will be made, except incidentally, and as I have in some respects modified my views as to the homology of certain of the parts, I will go into the entire subject in such detail as is necessary to prove my point; but without reprinting my first paper, which should be herewith consulted.

I do not expect denial at this day, when I claim that no explanation of the homologies of the mouth parts of insects can be considered satisfactory which will not stand the test of criticism by the theory of evolution. If we assume the origin of all insects from one original type, we must, necessarily, assume that all the mouth structures are derivatives of one type, and we must so study them as to be able to explain, step by step, just what specializations have occurred. We may not be able to complete entirely each link in the chain of evidence, but we can, at any rate, reach a result consistent with all the facts known to us. Any explanation which satisfies all the requirements of a regular and natural development is to be preferred to one which demands an unexplained specialization of any part, not in line with its function in other series. It is therefore necessary to study carefully the make-up of every separate mouth organ, and of every sclerite in each, to become thoroughly familiar with its uses and to ascertain the lines in which it varies or develops.

It may be premised that the mouth parts of the *Hemiptera* in their present condition are not included in the range of these studies. I have examined numerous specimens and have devoted especial attention to *Cicada* and *Thrips*—the latter classed as hemipterous for present purposes only—and I believed at one time that I had made out the remnants of a mandibular sclerite, and so published it. Mr. C. L. Marlatt questioned my conclusions and asserted that the mandibles are represented by one pair of bristles. While I believe that I was wrong in my identification of the mandibular sclerite, I am yet convinced that I am correct in claiming that beak and setæ are all maxillary structures. I have concluded, however, after a careful review of all my preparations and of what has been written, that the *Hemiptera* in the mouth structure are not descended from any well-developed mandibulate type, and that no trace of true mandibular structure occurs in any present form.

In other words, the *Hemiptera* equal all the other orders combined in rank, for all others are mandibulate or derivatives from a mandibulate type. The archetypal Thysanuran with undeveloped mouth organs varied in two directions—toward the haustellate type now perfected in our present *Hemiptera*, and to the mandibulate type: and there has never since been any tendency toward a combination. The haustellate type proved ill adapted for variation and there is, in consequence, a remarkable sameness throughout. This kind of structure must be studied on an entirely new basis to

get at the steps by which the present "beak" was developed, and my material is not sufficient for that purpose. The mandibulate type, on the contrary, proved well adapted for variation, and its differences and modifications are here traced.

For convenience, Kolbe's figures of the mouth parts of a grasshopper are reproduced on Pl. III, Fig. 22, and may be referred to in connection with the following explanation.

In a well-developed mandibulate mouth we have, forming an upper lip, the labrum, often notched in front or toothed: but never a paired organ, never with appendages, and never mechanical in function. It is articulated at base to the clypeus and serves to shield or protect the mouth in front; as a matter of fact, not a functional mouth structure at all. It is marked *lbr* in all figures.

More or less intimately associated with it on the inner side is the epipharynx, which is compared in function with the palate of vertebrates, and is furnished with sensory hairs, pegs or pittings. It may be so closely united with the labrum as to form, practically, a part of it, or may be entirely free. If free from the labrum, the epipharynx is more closely united with the other mouth parts, and in such cases its supports go to the mentum or labial structures. Not infrequently it has attachments to both. In form it may be a mere pointed process, or it may be a more or less divided, plate-like organ; but its functions are gustatory or sensory in all cases—it never becomes a functional mechanical structure, and I have never found it without a more or less developed labrum to shield it. It is lettered *epi* in all figures.

Just below these covering and gustatory organs is a pair of mechanical structures —the mandibles—set, one on each side of the head, and attached to the inferior margin of the epicranium or an extension from it. These mandibles are never jointed, rarely bear appendages, and never such as are functional, rarely have a movable tooth, and are usually solid and highly chitinized. They are actually made up of a number of sclerites, laterally united, but distinguishable in certain types like *Copris*, Pl. I, Fig. 8. I have elsewhere named and homologized these sclerites: but as the matter is not in dispute, and of no importance here, a simple reference to the figure in which they are named is all that is necessary. The position of this pair of mouth structures is invariable. They are completely disassociated from the maxillary or labial structures and remain attached to the head when all the other parts are removed in a body. They attach by socket joints to the epicranium and their tendons and muscles attach to its inner surface. They never change in function, never become united with or attached to the other mouth organs and never become internal structures. When not needed for chewing or biting the tendency is to obsolescence; never toward a change into a thrusting or piercing organ, so far as my observations extend.

Below the mandibles are found a pair of maxillæ, made up in all cases of a number of sclerites, and nearly always supplied with palpi or jointed tactile organs. The more particular consideration of these organs and their parts may be somewhat deferred.

Forming the lower lip and closing the mouth inferiorly is the labium, also made up of a number of sclerites and usually furnished with palpi. It is never entirely paired in existing insects, but is assumed to be made up of two more or less united structures, similar in essential character to the maxilla, as has been well stated by Prof. J. H. Comstock. This labium is an exceedingly important structure and forms the oral termination of the digestive tract or the mouth of the œsophagus.

Attached to the inner surface of the labium is the hypopharynx, a variably developed structure, which is supposed to be the remnant of another originally paired organ, the endo-labium. I have never seen the genera in which it is said to be well developed, hence have no well-founded opinion to offer. I find it uniformly a single organ, often highly developed and gustatory in function, sometimes a merely passive structure more or less closely attached to the ligula, usually very near the opening into the digestive tract.

Briefly recapitulated, the insect mouth, when most fully developed, consists of two pairs of lateral jaws moving in a horizontal plane between an upper and a lower lip, which are furnished with gustatory structures forming the roof and the floor of the mouth respectively. This mouth is adapted for biting and chewing and varies to types adapted to lapping, to sucking only, and to piercing and sucking. The problem before me is to ascertain by what modifications these different changes in type have become established.

If we examine the head of a well-developed mandibulate insect from the under side—*Copris carolina*, Pl. 1, Fig. 7, may serve as type—we find, centrally, the gula or throat, bounded laterally by the genæ or cheeks, extending to the posterior margin of the head and bearing anteriorly the labium. The labium when carefully dissected out is found to consist of a broad basal plate, the submentum, more or less firmly articulated to the gula and never, in existing insects, a paired organ. It bears anteriorly another plate, the mentum, also a united organ, though sometimes traces of a division are apparent. It is usually smaller than the submentum, sometimes membranous, often entirely separated and frequently so united with the latter part that the two are not separable. Though the submentum is the most persistent and dominant structure it has been customary to use the term mentum to apply to the united sclerites, and it will become convenient for me to so use the term hereafter when no confusion or misunderstanding can be occasioned. The structure is lettered *m* in all the figures.

Attached and articulated to the mentum anteriorly are the central ligula, a pair of paraglossa bounding it, and a pair of palpigers, one at each outer edge, bearing the labial palpi.

The ligula or glossa, marked *gl* in all the figures, is a paired organ only in the more generalized orders, and is usually present as a single, central structure, which may be either chitinous and rigid or membranous and flexible. It is the most persistent of all the labial structures, is never attached except to the mentum, and always has associated with it the hypopharynx where that is present. We always find at its base the opening into the alimentary canal, or œsophagus, as this part of it is termed, and this must ever be the test of labial structures—that they are attached to the mentum and have at their base the opening into the alimentary canal. The association is never broken, and the base of the ligula, whatever its form or however it is modified, always marks this point. On the other hand, by tracing the alimentary canal to its external opening, we can always recognize the ligula by its position, however little it may resemble normal types.

The paraglossæ are sometimes intimately united with the ligula, sometimes completely separated from it: they may be of the same or a different texture: but they always arise from the mentum on each side of and close to the central structure. Their tendency is to obsolescence, but they may become united and form a bed for the ligula which remains the inner organ. Their range of variation is not great; they are never jointed, and never become mechanical structures.

The palpi are tactile in function under all circumstances, though they may lose this function in great part and may, by coalescence, form a sheathing to the ligula. They are never, under any circumstances, attached anywhere except to the mentum, directly or indirectly, and their location must be constantly the same. They cannot, without losing their essential character, become disassociated from the mentum, nor can they ever form an envelope or covering for it, or for the submentum, without a change entirely at variance with any reasonable theory of development. To accomplish this they would first lose their character as labial appendages. In brief, the labium is the external beginning of the alimentary canal, and none of the parts ever lose this association. Whatever their modification, no labial structures can ever be joined to the sides of the head outside of mandibular or maxillary structures.

As an illustration of the most generalized form of labium at present known to me, the roach (*Periplaneta orientalis*, Pl. II, Fig. 16) may be selected. Here we find the mentum with a well-defined impression resembling a suture, and bearing a broad paired structure, from which arise the slender, two-jointed ligula, the broad, fleshy

paraglossæ, and the three-jointed labial palpi. This generalized structure fixes the relation of the parts, and from it we may pass to more specialized types.

In *Harpalus caliginosus* (Pl. III, Fig. 7) we have a case where the ligula forms a single, central organ, laterally bounded and on one side completely enveloped by the softer paraglossæ. The location of the palpi remains essentially the same. We have here two cases showing the change of a two-jointed membranous paired organ into a single, rigid, chitinous structure, and the identity of the parts is not questioned, nor I believe, questionable.

If we carry our dissections one step further and from the fresh specimen remove not only the highly chitinized parts, but also the softer attached structures, leaving maxillæ and mandibles undisturbed, we find in all cases the œsophagus in the cavity below the mentum and submentum, and these sclerites afford attachments for necessary muscles. They also form, by means of chitinous extensions and processes, a chamber or cavity protecting the œsophagus and supplying muscular attachments when a sucking or pumping structure is needed. Thus the mentum and submentum, whether separated or united, are always inferior coverings to the œsophagus. To support this structure, processes sometimes extend almost or quite to the upper or anterior surface of the head, and in many cases, where the epipharynx is separated from the labium, it is connected by means of long processes with the mentum. This is true in many Coleoptera, quite usual in the Hymenoptera, and occasionally found also in the Diptera. In Pl. I, Fig. 6, is a lateral view of the labium of *Copris carolina* when completely dissected out, and the clubbed processes, loosely attached to the inferior prolongation of the submentum, normally support the epipharynx. In Pl. I, Fig. 9, and Pl. II, Fig. 18, we note similar processes in *Andrena vicina* with part of the epipharynx still attached, and in *Polistes metricus*, where the structures are complete. Precisely the same structures occur in *Simulium* (Pl. I, Fig. 1^{d}), as will be more fully noted hereafter. It may be stated that I have adopted the term "fulcrum," used by Macloskie and others, to designate the structure formed by the mentum and submentum and containing the beginning of the alimentary canal.

In *Polistes metricus* (Pl. II, Fig. 18^{b}) I show the labium completely dissected out, with all its attachments, viewed laterally. It will be noted that here the mentum and submentum are united, highly chitinized, and form a scoop-shaped structure, bearing at one end the labial structures and enclosing normally the beginning of the œsophagus. Attached by long chitinous rods to the posterior angles is the epipharynx, so that hypopharynx and epipharynx are borne on the same base, are closely opposed to each other and may be manipulated by muscles arising close together. The origin of the palpi is shown from the mentum. On Pl. II, Fig. 18^{a}, are shown ligula

and paraglossæ of this same *Polistes*. The structures are here membranous, somewhat bladder-like, and well adapted for lapping by means of flattened, bent processes, set in series on the entire inner surface. The paraglossæ are completely separated and the mouth opening is shown at the base of the figure, as well as the chitinous ring marking the beginning of the œsophagus.

In *Andrena vicina* (Pl. I, Fig. 9) we find a similar yet quite different structure, *i. e.*, the same parts, used for much the same purpose, yet considerably modified in detail. The mentum is here much longer, more shallow, but similarly bears the epipharynx on chitinous rods. The ligula is more inflated and the paraglossæ are much reduced, but the palpi originate as before, and we have simply an illustration of the variation in form found in this united mentum and submentum. It is important to note here that in *Polistes*, *Andrena*, and indeed the Hymenoptera generally, the labial structures are free from all lateral attachments to the head and may sometimes be projected forward quite a distance. The attachment to the head, indeed, is muscular and membranous entirely, and there is no direct articulation to any point by chitinous or rigid processes. There is nothing therefore to prevent the growth of the head sclerites around the mentum, which would thus become an internal structure—as has actually happened in the Diptera.

Another feature upon which Dr. Packard rightly places great stress is that a salivary duct opens into the hypopharynx at the base of the ligula, which he thereby identifies. As this ligula is always attached to the mentum, it follows that this structure may be identified in the same way, while no structures not originating from the same point can be labial in character.

Before studying further the specializations of the labial structures, it may be well to say that they sometimes tend to become useless or obsolete, or so much reduced that they are difficult of recognition; and, curiously enough, in such cases the palpi seem to be the persistent organs. Thus in some species of *Scoliida* among the Hymenoptera the mentum bears only little, feebly developed palpi. A striking case is in the Panorpidæ, where on Pl. III, Fig. 4, the mouth structures of *Bittacus strigosus* are shown. Here ligula and paraglossæ have disappeared entirely; but the palpi are distinct and the curiously developed hypopharynx marks the beginning of the opening into the œsophagus.

A modification of this type is to be found in the Lepidoptera, where practically in all cases the palpi alone, attached to a plate of variable size and shape, represent the labial structures.

It seems a long jump from the reduced type in *Panorpida* to the fully developed labium of the *Apida*; yet, except for the fact that all the parts are much elongated,

there is no difference from *Andrena* or *Polistes*, which have been already studied. I have found no species which shows all the parts more fully developed than *Xenoglossa pruinosa* (Pl. II, Fig. 15). Here all the parts are equally developed and all are functional; hence it makes a good starting point. The mentum is not shown in the figure except at the point to which the other parts are attached, and surmounting it centrally, we find the ligula; here a united, though extremely flexible organ. Lying centrally upon it, so as to close a groove, is the hypopharynx, in this case not easily separable from the ligula. Arising close to the central organ on each side are the paraglossæ; almost as long as the glossa itself, flexible, unjointed, flattened and a little incurved at the margins so as to form, when closely applied to it, a partial shield for the ligula. Outside of all, situated at the outer margins of the mentum, are the palpi. These are four-jointed; but the basal joints are enormously elongated in proportion to the terminal two, and they are also flattened out, broadened and infolded, so that when at rest they cover and almost conceal the other labial parts, though not extending forward as far as they. In this insect the structures just described are almost entirely covered by the maxillæ, and a transverse section (Pl. II, Fig. 15ª) is interesting and instructive. It represents the structure at about the middle of the combined maxillæ and labium and illustrates the relative position of the parts.

The tendency in the bees is toward a loss of the paraglossæ, which shorten gradually until they disappear altogether, as represented in a species of *Bombus* figured in Pl. III, Fig. 15. Every intergrade is represented in any good series of bee mouth parts, and in their rudimentary condition, without function, they appear in *Bombus* sp., represented on Pl. III, Fig. 6. The palpi retain their unique development, and in the figure just cited are seen to be as long as the ligula itself, the basal two joints enfolding it almost completely, while the terminal joints are much reduced in size and set near the tip of the second joint, on the outer side. In other species these terminal joints are proportionately yet more reduced and are sometimes difficult to find. The essential point to be noted is that at their best development the paraglossæ are not jointed and that they tend to complete obsolescence in the most highly specialized types. The palpi in *Bombus* require a little further examination: Reference to the figure last cited will show a short segment between the mentum and the first long joint, and this is membranous in texture. The mouth parts in *Bombus* are folded when at rest and the hinge is at the mentum; hence the necessity for some such provision to enable the palpi to bend safely.

Now let us assume that the ligula of this *Bombus* became rigid and chitinized, and that the edges of the palpi enfolding it became united to form a complete cylinder; and then let us examine *Eristalis tenax* (Pl. III, Fig. 5) in the light of this assump-

tion. First let me say that I have already shown that a change from flexible to rigid ligula is not uncommon, and the suggested union of the palpi is a much less violent requirement than that imposed by the current explanation of the Dipterous mouth. Referring for a moment to Pl. I, Fig. 3, we see the entire mouth structure of *Eristalis tenax*. Above is the mentum and submentum, very like the structure already described for *Polistes* and entirely homologous with it, and at its tip we find arising in a group the structures further enlarged at Pl. III, Fig. 5. Centrally we find the now rigid ligula, deeply grooved in the middle, the channel closed by a flattened, also rigid and chitinized hypopharynx. Loosely enveloping this central ligula is a more membranous cylinder, evidently made up of two lateral halves, two-jointed, and the terminal joints separated or paired except at the base. As in *Bombus* the mouth of *Eristalis* is hinged, and the joint is also at the base of the ligula. The latter organ is so articulated as to allow of the flexion: but in the palpi we find again the provision already noted in *Bombus* a flexible, membranous, pseudo-segment. Now if we section the *Bombus* and *Eristalis* at the middle, we find the cuts alike, except that in *Eristalis* the palpi are completely united over the hypopharynx and closely approximated at the opposite side. If we section near the tip, the cuts in both cases are identical. That this united structure in *Eristalis* is the united labial palpi seems to me beyond doubt. In the first place, the point of origin is normal, next to the ligula and at the tip of the mentum; and, secondly, it is a jointed organ and therefore cannot be paraglossa. It is in all points the structure of *Bombus*, with the terminal joints lost and the two halves united for the greatest part of the distance. That the parts named mentum and submentum are really such, is proved by the fact that the hypopharynx, which is not in dispute, originates from and that the œsophagus originates within it.

In *Bombus terricolus* the ligula is unusually developed and much longer than the labial palpi, while the paraglossæ are wanting. In Pl. III, Fig. 12, is a *camera lucida* sketch of the labial parts of a carefully mounted specimen. The structures here are exactly as normally held when at rest, and only the mentum is a little crushed by the cover glass on the shallow cell. Now chitinize this whole structure thoroughly, and then compare with the drawing of *Chrysops vittatus* (Pl. III, Fig. 13) made in the same way. The magnifications are different, of course, the *Bombus* being drawn at short range with a four-inch lens while the *Chrysops* was drawn at long range under a one-inch objective. The object was to get the two of approximately the same size for convenience of comparison. In the Tabanids the mouth parts are rigid and not flexed, and no sort of joint or hinge is required; hence the structures are all rigidly united at the base to the mentum. In *Bombus terricolus* the palpi are reinforced by a heavier

chitinous rod a little to one side of the middle, and just this sort of structure we find everywhere in the Tabanids, lying outside of the ligula at base, articulated to the outer edge of the mentum. This, in fact, first led me to suspect the true nature of the structure. If now we section *Bombus* and *Tabanus* near base, the cuts will be alike, save that the palpi in the latter are united at one margin. If the cuts are made toward the tip, the sections are alike—ligula and hypopharynx alone appearing in both cases. We have then, in *Chrysops* also, a complete labium, save that the paraglossæ are absent and the palpi are united on one edge.

In the *Simuliidæ* are many interesting species with generalized mouth structures, and of these I have studied the "Buffalo gnat," from material kindly furnished by Dr. Riley, an undetermined *Simulium* sent me in numbers by Prof. Aldrich, and an undetermined little midge collected by me at Anglesea, N. J. The species are practically identical in the labial structures, and here again the mentum and submentum strongly recall *Polistes* and other Hymenoptera. The hypopharynx is well developed and the ligula are nearly divided; but I have no satisfactory sections of this insect and the relations of the parts are not clear to me. At Pl. I, Fig. 1^{b}, the labium of the "Buffalo gnat" is shown. In the species sent by Prof. Aldrich I succeeded in getting a dissection illustrating the connection of the epipharynx with the mentum, and this is illustrated at Pl. I, Fig. 1^{d}. This is really an exceedingly interesting specimen and it clears up the relation of the frontal prolongation of the mouth. That the structure so labeled is really the epipharynx there is little room for doubt, and the location of the little, chitinous, toothed processes, and their character, leaves no doubt in my mind that they are mandibular rudiments—exactly as I claimed in my first paper. That they can be dermal appendages, as has been claimed, does not seem reasonable to me. They are too highly chitinized in comparison with their surroundings, and why should they so completely resemble miniature mandibles? I do not know of any case of dermal appendages of a similar character, and it is at least passing strange that such should be developed exactly where, normally, mandibular rudiments might be reasonably expected.

The tendency in the piercing Diptera is constantly in the direction of simplicity of labial structures, and so we gradually note the loss of all trace of accessory labial structures, leaving the ligula and hypopharynx as sole representatives. In the *Asilidæ* there are no other attachments to the mentum, as shown in Pl. III, Fig. 1^{c}.

These apparently single structures are sometimes interesting in section, as appears in *Stomoxys calcitrans*, Pl. I, Fig. 11. Here the cut shows two crescent-shaped structures connected at one edge by the thinnest kind of a chitinous shell, and closed opposite by a hypopharynx, which is almost tubular in structure.

Very interesting is the modification found in the *Empida*, illustrating the extreme in the loss of parts: for here the hypopharynx is also wanting, though the salivary duct remains, opening into the grooved ligula, as shown in Pl. III, Fig. 2[b]. In this case the hypopharynx is replaced by an extension and peculiar modification of the labrum. This sclerite is elongated so as to extend to the tip of the labium, and is very much dilated, somewhat bulb-like at its base. In Pl. III, Fig. 2[a], labrum and ligula of *Rhamphomyia longicauda* are seen from the side, while in Pl. II, Fig. 13, are shown the same structures in *Empis spectabilis*. The edges of the labrum are turned under sufficiently to leave a central channel just large enough to receive the ligula, with which it then forms a closed tube through which the food is taken.

In most of the Muscid flies we find a structure approximating *Eristalis* with the labial palpi removed: and the parts may be longer, or shorter, or differently developed, while adding nothing to what has been already shown; they are, essentially, reduced piercing structures, no longer functional.

We have, however, in certain other species, where the mouth structures are short, very poorly developed labial structures. So in *Hermetia mucens* (Pl. III, Fig. 14) the broad and large mentum bears only a short, scoop-like ligula. The specimen from which the figure was made was somewhat distorted in mounting and the ligula is turned just half round. Similar structures occur in the *Bibionida*, and *Eupsychus bellus* (Pl. I, Fig. 12) is not essentially different.

Heretofore the hypopharynx has been referred to mainly in species in which it was feebly developed and played but a passive part as a covering structure. It is sometimes a highly specialized sensory structure, though it varies greatly, even when functional.

A very curious type is found in *Bittacus* (Pl. III, Fig. 4[a]), where it takes the form of a simple cylindrical process, set with spines, almost like an odd joint of some slender palpus. In *Copris carolina*, Pl. I, Fig. 1, showing the epipharynx, may be accepted as a fair representation of the hypopharynx as well, save that the latter is on a much reduced scale. The opening of the salivary gland is in a dense mass of specialized spinous processes.

In the *Libellula*, among the dragon flies, we have an inflated, somewhat tongue-like organ (Pl. I, Fig. 10), in which the salivary duct is plainly traceable to its opening among a mass of crossed, specialized spines. The surface is richly supplied with sensory pittings and tactile hairs. It is a great modification from a structure of this kind to the simple, ribbon-like form of *Bombus*, or the flat, slender, chitinous form in *Tabanus*: but the intermediate stages are all present.

To recapitulate concerning the labial structures. The mentum and submentum

cover the œsophagus. They may be united so as to form a single organ, and their tendency is to become internal head structures. The ligula has at its base the opening into the alimentary canal; it is rarely paired, may be rigid or flexible, and has closely associated with it the hypopharynx, recognizable by the salivary duct which it shelters. The paraglossæ arise on each side of the ligula or glossa, and may be chitinous or membranous. They are never jointed, never developed for any specific mechanical purpose, and their tendency is to become obsolete. The labial palpi are essentially tactile and never become mechanical save as they may form a covering or sheath for the ligula.

From the most generalized type found in the *Blattidæ* the modification is first from a divided to a single ligula; next to a disappearance or obsoleseence of the paraglossæ; later the labial palpi also disappear, and finally the hypopharynx is also dispensed with. There is no break, and nowhere is there any violent change of structure or function.

We are now ready to take up the maxillæ, which, though composed of a larger number of sclerites, are usually more easily understood in the ordinary type of mandibulate insect. The organ is usually paired and never so completely united as the labial structures. The two parts are always external to the labium, which it is their tendency to enfold, and they never have any direct connection with the alimentary canal. Though the maxillary structures tend to form a covering or sheath for the labium and its appendages, there is never any intimate connection between them. No part of the maxilla ever unites with any part of the labium or with any of its appendages. The maxillæ are essentially mechanical structures, and their range of variation is sufficiently great to meet the most diverse possible demands made upon them. A distinct and fundamental characteristic is the fact that each set of sclerites has its own peculiar possibilities and limitations, and once these are understood the most highly specialized type becomes simply explicable.

On Pl. III, Fig. 17, is a copy of Prof. Comstock's figures of *Hydrophilus*, showing the maxilla from both surfaces, and these may conveniently serve as a text to explain the sclerites composing it. At the base is the cardo or hinge, giving attachment to muscles and tendons articulating it to the head. It is to be noted that there is no firm or chitinous articulation to any head sclerite, and except by muscles or tendons no direct attachment. This we found the case also in the labium in the more specialized forms, and in the Hymenoptera, for instance, labium and maxillæ together are easily dissected out without cutting any but muscular tissue, and without breaking any chitinous connections or joints. This is in marked contrast with the mandibles which, when functional, are always firmly articulated by chitinous joints to the external

head sclerites. Supported upon the cardo is the stipes or foot-stalk, deriving its muscular attachments largely from the cardo; but to some extent from the head itself, and this feature is a variable one. Surmounting the stipes is a palpifer or palpus-bearer, to which is attached a palpus, varying in the number of its joints. This derives all its muscles from the stipes in the typically developed maxillæ. On the inner side of the stipes is attached the subgalea, deriving its muscles from the head in large part; and this bears a two-jointed galea or hood. It is a matter of some importance to note that this galea is never more than two-jointed under any circumstances, and that the tendency is to maintain that number; though in many instances it is reduced to one only. It is the most persistent as well as the most variable of the maxillary structures, and is present when any of them exist at all. Inside of the subgalea, and attached to it as a rule, is the lacinia or blade, which may or may not bear a digitus or finger. In the figures just cited we find what may be termed a normal or proportionate development of all the parts, in which no one sclerite is unduly developed or specialized. Before attempting to study specializations it is important to note that, when carefully examined, the sclerites are seen to be arranged in three parallel series. That is to say three separable parts have grown together laterally, and this union bears with it the possibility of future disunion or separation for special purposes. We have as the inner series lacinia and digitus; as the middle, subgalea and galea; and as the outer the cardo, stipes and palpifer with the attached palpus. Now if we examine some of the Neuroptera, *e. g.*, *Sialis* (Pl. III, Fig. 16), we find this lateral arrangement very strongly marked, and it is easily understood that each of these parallel sets may have their own peculiar limitations, and that each may be separately and independently modified.

But lest this seem, after all, a far-fetched conclusion, let us examine the maxillæ of *Bittacus strigosus* (Pl. III, Fig. 4′), and we find almost exactly the hypothetical state of affairs actually existing! Lacinia, galea and palpifer all separated, of nearly equal length, but of quite different appearance. The appearance of a transverse section made at about the middle is shown as Fig. 4. For a generalized type this form is especially valuable, and we may fairly use it as a guide in our discussion of maxillary possibilities.

There is no absolute rule in the matter, but usually the galea tends to become the dominant maxillary organ. In many Neuroptera, and especially in their larval stages, the laciniate structure is best marked, as illustrated in Pl. III, Fig. 9, representing the maxilla of a Perlid larva. Here the galea is reduced to a subordinate rank, and in many predaceous Coleoptera it is truly palpiform.

In many Orthoptera the development of the galea justifies the name by forming

an almost complete hood over the lacinia. This is well illustrated in the maxilla of the oriental cockroach, *Periplaneta orientalis*, shown at Pl. III, Fig. 8. At this point a comparison of the figure just cited with the galea of *Simulium* (Pl. I, Fig. 1[c]) will prove interesting and instructive.

In the Hymenoptera the galea dominate throughout: no elongated palpifer is ever developed, and indeed the maxillary palpi are sometimes almost rudimentary in the Apidæ, as shown at Pl. III, Fig. 15.

In *Polistes*, illustrated at Pl. II, Fig. 18', we find a common type of the *Vespidæ*, where the lacinia forms a small, blade-like structure, free for almost its entire length, and the maxillæ as a whole shelter a large part of the labium. In those cases in which the "maxillæ" are elongated, the galea is usually the organ affected.

Thus in many Meloids among the Coleoptera we have the mouth parts elongated, and a study of the maxilla of *Nemognatha* (Pl. III, Fig. 20) shows at once the sclerites concerned. Here the lacinia is much reduced, and if we remove it altogether we have the normal Lepidopterous maxilla, which tends to a locking together to form a complete tube. Recently it has been found that in certain Lepidoptera the lacinia are actually present, and the figures which I have seen indicate a structure in all essentials like that of *Nemognatha*.

While speaking of the Lepidoptera it may be well to cite *Pronuba* (Pl. III, Fig. 21), in which the palpifer is elongated in the female and highly specialized into a sensory and tactile structure, though unjointed. In a well-prepared specimen the point of origin is perfectly clear, and it is entirely homologous with the structure seen in *Bittacus*. In the male (Pl. III, Fig. 19) the "tentacle" is not developed, though the palpifer is enlarged to some extent.

In the *Apidæ*, among the Hymenoptera, the lacinia disappear entirely in extreme cases, or are at least greatly reduced, while as already stated the palpi are sometimes scarcely visible. The galea, on the other hand, is very prominently developed, and when at rest envelopes the ligula and paraglossæ almost completely. In Pl. III, Fig. 15, is represented the usual appearance of all the parts separated, while at Pl. II, Fig. 15', the transverse section of the mouth structures of *Xenoglossa pruinosa* shows their normal relation when at rest. It is seen that the galea actually overlap somewhat at one margin, and a union along this line would be scarcely considered a violent stretch of the range of variation. Assume such a union, eliminate the paraglossæ which are organs tending to obsolescence, and then compare with the transection of *Eristalis tenax* (Pl. I, Fig. 3'). If the palpifer be eliminated from this latter figure the cuts are practically identical.

Returning to our figure of *Bombus* (Pl. III, Fig. 15), we note at the outer edges

of the galea a series of ridges which, under a high power, look extremely suggestive of the structures found in the labellæ of Diptera, especially where, as for instance in *Bombylius*, the pseudotrachea are imperfectly developed. These ridges vary much in the species; but are particularly marked in a little *Andrena* near *vicina*, if not that species itself. Here we see (Pl. III, Fig. 3) the entire inner face clothed with a thin membrane which is crossed by numerous closely set fine chitinous lines! I claim that this structure is the homologue of the pseudotracheal structure in the Diptera, and that in the latter order it is in the galea that the development occurs, as it does here in the Hymenoptera. The relative differences in size are not of importance. As to the particular use of this structure in *Andrena* I have no suggestion to make.

In the Proceedings Ent. Soc. Washington, Vol. III, Mr. Ashmead figures on Pl. III, some very suggestive mouth structures of parasitic Hymenoptera, of which that of a Pteromalid is reproduced on Pl. III, Fig. 18. The central labium with its attached structures is much reduced in size, and the maxillæ, bearing the well-developed palpi, are reduced to a single structure, the galea, resting upon what may be considered the stipes. Now if we bring these two parts of the maxillæ a little more closely together, we have almost the exact structure seen in *Bibio* (Pl. III, Fig. 11). The basal ring, bearing the palpi, corresponds almost exactly to the basal ring of *Pteromalus* except for size, while except that the surmounting galea are two-jointed, the correspondence with the upper portion of the structure is equally marked. The labium in *Bibio* is much like that figured in Pl. III, Fig. 14, for *Hermetia*, and in Pl. I, Fig. 12, for *Eupsyllus*.

I am making no very risky statement when I assert that the sclerite to which the maxillary palpi are attached must of necessity be maxillary; and further, it is equally safe to say that no maxillary sclerite can bear a labial appendage: and certainly not a labial palpus. It would be an absurdity, contrary to all the laws of a natural development, for a modified labial palpus to become attached to the sclerite bearing also the maxillary palpus: while if we consider it the two-jointed galea, its position is normal, requires no assumption of change or character, and does not differ in any essential points from the gale of the roach (Pl. III, Fig. 8). Yet these two joints in *Bibio* will, with a ridged membrane thrown over them, represent the labellate tip of the Muscid proboscis. That such a ridged membrane is well within the range of galeal variability we found in the *Andrena* near *vicina* (Pl. III, Fig. 3).

The structure in *Eupsyllus bellus* (Pl. I, Fig. 12) resembles *Pteromalus* yet more closely, in that a single ring only surmounts the segment bearing the palpus. In this instance the maxilla is reduced to exactly the same segments seen in the Hymenopteron, and logic demands that we recognize them as the same. In this case, how-

ever, the lower ring is complete—*i. e.*, the two halves of the stipes have become united. That it must be stipes is shown by the fact that it bears the palpus, and again the surmounting sclerite must be maxillary also.

There are other species allied to those already cited in which similar structures occur; but I need for the present call attention to only one more: a species of *Olfersia* (Pl. II, Fig. 19). Here the ring is complete in front, but broadly open behind, and bears the chunky, single-jointed palpus. Surmounting is a single sclerite, very much resembling in appearance that of *Pteromalus*, and undoubtedly homologous with it. Of course *Olfersia* is parasitic in habit, and the mouth parts are specialized for blood-sucking; but the sclerites composing them are nevertheless derived from the same source as in the "higher" types.

I have several times referred incidentally to *Simulium*, and of this the galear structures are figured (Pl. I, Fig. 1^{a}). Dissecting the parts out carefully we find an almost complete ring at the base, the stipes, to which the palpus and palpifer are attached. Surmounting this is a pair of sclerites, each almost a half cylinder, representing the subgalea, and bearing the two-jointed galea. Here again I claim that the three joints just referred to *must* be maxillary because they are directly articulated to the sclerite bearing the maxillary palpi, and the labial structures are all shown at Fig. 1^{b}.

A step in the direction of union we find in the Anglesea gnat or midge—also a Simuliid, to which reference has been already made. Here we see (Pl. I, Fig. 2^{a}) the subgalea united most of their length at one side, while the galear joints are yet free. The basal stipes is not figured because none of my specimens showed it clearly; but the palpifer, palpus and lacinia, as they are connected with it, are shown in the specimen.

In the *Asilidæ* we find another suggestive structure, studied in the light of the facts already set out. Here we see, as illustrated Pl. III, Figs. 1^{a} and 1^{b}, the basal stipes well developed, united posteriorly, but separated in front. The palpifer and its attached palpus are situated at the sides, clearly articulated to the stipes, whose character is thus fixed. Attached to this stipes is a broad, infolded structure, united behind but open in front; maxillary because of its attachment to the stipes, and subgalea from its location. It bears in orderly sequence the two-jointed galea of which the terminal joints are free. The species of the *Asilidæ* are large and easily dissected, and the figures were drawn from a species of *Laphria*. The attachments are but little different in the species, and as the figures illustrate the structure from both front and rear, the position of the joints should be clear. These figures will be again referred to in another connection.

In all the species heretofore cited the galear joints were more or less distinct and the pseudotracheal system was little or not at all developed. As the face of the joints becomes covered by a ridged membrane the texture of the entire structure changes. It becomes less chitinized, and the chitine is not evenly distributed, causing sutures to become indistinct and poorly marked. Yet, keeping in mind the general line of variation, we can usually reach a correct conclusion.

In a Leptid, species unknown, we find the appearance shown in Pl. II, Fig. I. Here there is a united basal plate, covered on one surface with a membrane, and from the chitinous portion arises the palpifer with its attached palpus. Surmounting the chitinous base are two joints, the galea, the chitinous parts of which only are shown in outline, the balance of the space being covered by membrane. Here again the attachment of the maxillary palpus to the basal sclerite determines the maxillary character of all the sclerites directly articulated to it.

In *Hermetia illucens* (Pl. II, Fig. 17) the entire structure is much more membranous, yet the basal chitinous plate is paired, and while the parts are shown in a distorted position, the two galear joints and their relation to the basal, palpus-bearing structure is yet perfectly obvious. The other maxillary structures have completely disappeared, while what is left of the labium is seen at Pl. III, Fig. 14.

The mouth parts in some species of *Tipula* are interesting, and a fair illustration of one of the "snub-nosed" species is seen at Pl. I, Fig. 5. Here the origin of the palpus at the immediate base of the chitinized part of the labella indicates its character, and if we divest the chitine of the surrounding membrane we get the appearance shown at Fig. 5'. Practically we have a completely paired organ, the relations of which are perfectly simple when the confusing and unimportant membrane is removed.

The peculiar relation of labrum and labium in the *Empida* has been already noted, and this makes it easy to separate off all the other parts adhering to the margin of the head, but not in any way connected with the labium. The relation of the parts to each other in *Empis spectabilis* is shown on Pl. II, Fig. 13, while on Pl. III, Fig. 2, are shown the maxillary structures of *Rhamphomyia longicauda*. In this latter figure we note that the parts, except palpifer, are entirely membranous. From the basal sclerite the palpi arise so as to form only a continuation of the membrane itself with an extremely slight attachment to the chitinous palpifer; and to this very same membrane there is articulated by a slightly thickened suture the subgalea, united posteriorly, but separated in front; and this bears in turn the indistinctly segmented galea. This entire structure obviously belongs together and is one organ—necessarily the maxilla.

A very similar structure is found in *Chrysops* (Pl. II, Fig. 14) and in other species

of the *Tabanidæ*. Now it will be remembered that in this genus I showed the connection of all the labial parts with the mentum, where they normally belong; hence all the other parts must be, of necessity, maxillary. So we find also in Pl. II, Fig. 14, that the central labellate structure, two of the piercing structures and the maxillary palpi all arise from a single united basal sclerite, the stipes.

In *Eristalis tenax* (Pl. I, Fig. 3) these labellate structures are shown, turned aside to expose the labial structures. Here also I showed the presence of labial palpi in close connection with the ligula and hypopharynx, normally attached to the mentum, and again it follows that the other structures must be maxillary. Again also I must call attention to the fact that the palpi are mere continuations of the enveloping membrane, and that this membrane continues without break to the tip of the labella. Unless we are to believe that a continuous membrane may give rise to both the maxillary and labial palpi, we cannot possibly consider the labella as labial structures.

I have now traced out what seems to me a continuous development of the modifications of the subgalea and galea, and have shown, I think, that from *Pteromalus* in the Hymenoptera to *Eristalis* in the Diptera, a continuous chain may be constructed, requiring nowhere any change of character, function or location. No disassociation from other maxillary structures and no connection with labial structures.

In taking up the modifications of the palpifer I am confined almost entirely to the Diptera, in which this sclerite is best developed. In *Bittacus* I showed its development to an elongated structure of no particular type or function and of about the same texture as the galea. In *Pronuba* I showed its development into a highly specialized "tentacle," tactile and sensory as well as mechanical in character. In the Diptera it is quite usually present as an elongated, rigid, chitinous organ adapted for piercing. It occurs in all the piercing types and is present as a rudiment in many others. It undergoes a curious and interesting change in function as the Dipterous mouth changes from the piercing to the scraping or lapping type, and as it becomes flexed.

The simplest form occurs in those piercing Diptera in which the proboscis is not flexed. Thus in the Buffalo gnat (Pl. II, Fig. 9) it is a stout, semicylindrical piercing organ, enlarged both at base and at tip, at which latter point it is also toothed. The connection of the palpus with the subgalea was already shown on Pl. I, Fig. 1ⁿ, and this shows how the chitinous palpifer forms part of the combination. The palpifer arises, normally, outside of the galea; yet at the tip it is found in connection with all the other piercing structures inside of that organ. How it gets there is illustrated in the Anglesea Simuliid (Pl. I, Fig. 2ⁿ), where all the maxillary parts are shown in proper connection, and it is seen that the palpifer enters the galear envelope in the

incomplete articulation between galea and subgalea. By separating off the galeal structures, the relation of palpifer and lacinia in *Simulium* is illustrated (on Pl. I, Fig. 1), and the convergence of the two at tip is not distortion, though perhaps a little exaggerated by pressure. The result of this change of position is that a section made near the base of the proboscis would show as illustrated on Pl. I, Fig. 2, while one made nearer the tip would show as in Fig. 1'. Incidentally it will prove interesting to compare these sections with that of *Bittacus strigosus* (Pl. III, Fig. 1), leaving out of consideration the abnormal labium of the latter. The resemblance is perfect, and the resemblance expresses fully the actual condition of the matter. A very similar state of affairs exists in the *Asilida* (Pl. III, Fig. 1'). Here the palpifer is the only maxillary piercing organ, and the figure itself shows clearly how easily it would swing inside the ample space left in the subgalea for its entrance. The curvature of the organ is such, also, that when in place it meets the central ligula so as to form a solid puncturing organ.

So in *Chrysops* (Pl. II, Fig. 14) the structure is seen to be similar to that in *Simulium*: but here, as almost everywhere else in the order, it is cylindrical or nearly so, in marked contrast with the lacinia, which is always flattened.

As we get into types that have lost the piercing habit, the function of the palpifer fails or changes. If the species have a short, nonflexed proboscis, it simply dwindles from disuse. So in *Stratiomyia* and in *Leptis* (Pl. II, Figs. 1 and 2) it simply forms a little chitinous appendage to the palpus—a mere remnant without function. If, on the other hand, the species are able to flex the proboscis, another change takes place. There is needed then some lever to which muscles for flexing can be attached, and no structure seems to have been so easily adaptable as the palpifer. So we find in the *Empida*, where only slight flexion is required, only a small basal extension, shown at Pl. II, Figs. 4 and 3, for *Empis spectabilis* and *Euloncha tristis*, and at Pl. III, Fig. 2, for *Rhamphomyia longicauda*.

In the *Bombyliida* is a step forward. The insects are not predaceous, have the habit of hovering over flowers and using the proboscis in feeding in that position. This requires a much better control, and as a result the basal extension is much better developed, as shown in Pl. II, Figs. 6 and 7, illustrating *Bombylius* and *Anthrax*.

As we get into types like *Eristalis* and other *Syrphida*, the basal extension becomes the most prominent and the piercing portion diminishes in size (Pl. II, Fig. 5), and keeping step with this modification is a gradual separation of the palpus itself from the palpifer. This is well illustrated both in *Eristalis* and *Sphærophoria*, and this tendency continues until in *Lucilia* (Pl. II, Fig. 10) the separation is complete, though the piercing portion of the palpifer is yet distinguishable. In *Calliphora* even

this disappears and the chitinous rod is entirely disassociated from the palpus. Finally in *Stomoxys calcitrans* (Pl. II, Fig. 12) there remains nothing to indicate the existence of any relation between the slender chitinous rod and the distant maxillary palpus. It is not in the least strange that guesses as to the character of this structure in *Musca domestica* should have been so often wide of the mark; though with a proper series as now shown, its origin is clear.

There remains to be accounted for the lacinia, and this in the Diptera is the flat, blade-like structure generally identified as the mandible. It has been shown that while the lacinia is often the dominant organ in many mandibulate insects, the tendency is, on the whole, to a decrease in size, ending in the Hymenoptera in its entire elimination. In the Diptera it is present in the blood-sucking species only, and it may be identified by its position and its relation to the other maxillary structures. It has been several times referred to incidentally, and in the Anglesea Simuliid (Pl. I, Fig. 2^{c}) its relation to the other maxillary parts is shown. In Pl. I, Fig. 1^{c}, is illustrated the connection between the palpifer and lacinia in the *Simulium* sent me by Mr. Aldrich. This connection is not fanciful but actual, and no sclerite so intimately connected with an admitted maxillate structure can be anything but maxillary.

Again in *Chrysops* (Pl. II, Fig. 14) I have illustrated the fact that all the structures which I consider maxillary have a common origin. At Fig. 14^{c} I show the lacinia alone, and it is to be noted that at the base it is modified for attachment with reference to the palpus. Now unless this is a maxillary sclerite, why should it be modified to accommodate the maxillary palpus? Does it not seem rather absurd to believe that this can be a mandible brought to originate from one point with the palpifer and modified to allow it to envelope at base the maxillary palpus?

One of the most serious difficulties in the way of the proper understanding of the mouth parts of haustellate insects has been the desire to provide for the mandibles on the theory that they are among the permanent structures. Yet I cannot understand why this should necessarily be the case. When functional, mandibles are essentially chewing or biting organs, and when the insects do not require such structures, it seems to me most natural that they should become obsolete: and that is exactly what has occurred according to my reading of the facts. Their functional character never changes; they simply dwindle from disuse and gradually disappear. So we find them in the Lepidoptera as mere rudiments, connected with a highly specialized maxilla; and in the Rhynchophora they are sometimes mere remnants, occasionally reversed in position—exactly as I pointed them out in *Simulium*. I think that in view of all the evidence presented by me, none of the piercing organs of the Diptera can be considered mandibles, and I cannot even yet, after carefully weighing all that Dr. Packard

has written, see any reason why the rudimentary structures at the tip of the labral extension in *Simulium* are not mandibles.

If we refer back again for an instant to the Panorpids we note (Pl. III, Fig. 1) that in *Bittacus strigosus* the origin of the mandibles form an extension of a lateral head sclerite, with the labrum-epipharynx between them. In *Panorpa* the mouth structures are much shorter, set on an immensely elongated stipes, and at the tip of the frontal extension of the head we again have the mandibles, much reduced, with a small, lappet-like labrum-epipharynx between them. Now the situation of the rudiments in *Simulium* corresponds almost exactly with that of the undoubted mandibles in *Panorpa rufescens* (Pl. III, Fig. 4); but in the *Empida* we find a yet more closely allied structure. I have already called attention to the peculiar elongation of the front of the head in this family, and now if we examine this at tip, in *Empis spectabilis* (Pl. II, Fig. 13) its very close resemblance to *Panorpa* is at once evident. We find a central lappet-like structure with a sensitive surface, which looks like and logically should be the epipharynx, and moving below it is a pair of appendages which, in my opinion, represent mandibles. They are membranous and probably not functional: but this is no argument against their character. I believe that the similarity in the appearance between Pl. III, Fig. 4, and Pl. II, Fig. 13, is the expression of a true homology, and that mandibles in the Diptera exist in no other form or situation. It is likely that other species, showing them much more perfectly, will yet be discovered; but so indeed do I believe that labial palpi, properly connected with the mentum, will yet be found, so distinct in character that, even if not functional, their homology cannot be mistaken.

Labrum and epipharynx have been frequently referred to in the course of this paper, and in the introduction the general relation of these two parts has been explained. Both structures occur in many families of the Diptera. As in the case of the hypopharynx, the epipharynx has always connected with it a salivary duct. In its intimate connection with the labrum it is shown on Pl. I, Fig. 10, illustrating the epipharynx of *Libellula*. Here the chitinous tube giving passage to the duct is fully shown. As an example of a highly developed structure, the epipharynx of *Copris carolina* is shown (Pl. I, Fig. 1), and here the salivary duct opens among the dense central mass of spinous processes. The epipharynx of *Polistes* was referred to in the description of the labium, as was that of *Andrena* in the connection. In the Hemiptera the labrum and epipharynx are usually well developed and the salivary duct is in many cases very well marked.

Among the Diptera some of the larger *Syrphida* have the labrum quite distinct, and on the under surface is a sensitive surface into which an obvious duct, with chit-

inous protecting margins, is led, as shown on Pl. III, Fig. 10. A much better developed organ, strongly resembling that in some of the Hemiptera, we find in the *Asilidæ* (Pl. III, Fig. 1′), and here also the salivary duct is obvious. The structure in *Simulium* has been already referred to, as has that in the *Empidæ*.

To recapitulate concerning the maxillæ: The sclerites form three series, each of which has its own possibilities of development. The lacinia never develope into anything other than a chewing or piercing organ and always arises inside of the galea. The galea varies in the direction of forming an enveloping organ for all the other mouth parts, and the subgalea eventually unites along one margin for that purpose. There is a tendency to develop a ridged membrane on the inner surface of the galear joints which culminates in the pseudotrachea of the muscid labella. The palpifer has a small range of development, from an unjointed, flexible, tactile organ, to a rigid, piercing structure; and as this becomes useless, to a process for the attachment of muscles used to flex the proboscis.

It remains only to acknowledge the assistance received from my entomological friends. Dr. S. W. Williston has from time to time sent me such specimens as I thought might help me; Mr. C. W. Johnson has given me numerous species of families selected because of apparent differences in the mouth structure; and to Mr. J. M. Aldrich I owe many other species in some numbers, among them the Simuliid already referred to. Mr. E. P. Fell kindly sent me specimens of *Panorpa* and *Bittacus*, which enabled me to make a much more complete study of these insects than would have been otherwise possible. To all these gentlemen, as well as to the others who have in any wise aided me, I desire to express my thanks.

Concerning the figures—most of them are *camera lucida* drawings. A few are drawn from micro-photographs, assisted by the specimens themselves. The figures of transections are largely made from actual preparations; some are redrawn from other sources, while a few are ideal.

Explanation of the Plates.

The lettering of the parts, the same throughout, and the abbreviations, are as follows: *Lbr*, labrum; *epi*, epipharynx (the two sometimes combined as *lbr-epi*); *md*, mandible; *car*, cardo; *st*, stipes; *pfr*, palpifer, *mp*, maxillary palpus; *gal*, galea; *sg*, subgalea; *lac*, lacinia; *dig*, digitus; *sm*, submentum; *m*, mentum; *gl*, ligula or glossa; *par*, paraglossa; *lp*, labial palpi; *hyp*, hypopharynx.

Plate I.

Fig. 1. Buffalo gnat. 1ª, galear structures with palpi attached; 1ᵇ, labial structures; 1ᶜ, lacinia and palpifer of Simulium from Aldrich; 1ᵈ, labrum and labium of Simulium from Aldrich; 1ᵉ, transverse section through middle of mouth of Buffalo gnat.

Fig. 2. Simulium from Anglesea, N. J. 2ª, the maxillary structures in their actual relation to each other; 2ᵇ, transverse section of mouth parts toward the base of subgalea.

Fig. 3. Mouth parts of *Eristalis tenax*. 3ª, transverse section of same at the middle of subgalea.

Fig. 4. *Copris carolina*, epipharynx.

Fig. 5. Mouth structures of Tipula sp.; 5ª, the chitinous parts of the same.

Fig. 6. *Copris carolina*; labial structures dissected out and seen from side.

Fig. 7. *Copris carolina*: chitinous part of under side of head.

Fig. 8. *Copris carolina*; mandible with the sclerites named and homologized.

Fig. 9. *Andrena vicina*; labial structures, with part of epipharynx attached.

Fig. 10. *Libellula* sp. *a*, the epipharynx; *b*, the hypopharynx.

Fig. 11. *Stomoxys calcitrans*; transverse section through the middle of the ligula.

Fig. 12. Mouth parts of *Euparyphus bellus*.

Plate II.

Fig. 1. Maxillary structure of *Leptis* sp.

Fig. 2. Palpifer of *Stratiomyia*.

Fig. 3. Palpifer of *Eulonchus tristis*.

Fig. 4. Palpifer of *Empis spectabilis*.

Fig. 5. Palpifer of *Spharophoria cylindrica*.

Fig. 6. Palpifer of *Bombylius*.

Fig. 7. Palpifer of *Anthrax*.

Fig. 8. Palpifer of *Chrysops rittatus*.

Fig. 9. Palpifer of *Simulium*.

Fig. 10. Palpifer of *Lucilia*.

Fig. 11. Palpifer of *Calliphora*.

Fig. 12. Palpifer of *Stomoxys*.

Figs. 10 to 12 inclusive were accidentally reversed in making up the plate.

Fig. 13. Mouth parts of *Empis spectabilis*. 13ª, elongated head structure at tip, showing mandibles and epipharynx 13ᵇ, transverse section at middle of subgalea.

Fig. 14. Mouth parts of *Chrysops rittatus* showing maxillary structures attached together. 14ª, the lacinia; 14ᵇ palpifer and palpus; 14ᶜ, transverse section at middle of galea.

Fig. 15. Labial structures of *Xenoglossa pruinosa*. *a*, transverse section at about middle.

Fig. 16. Labial structures of *Periplaneta orientalis*.

Fig. 17. Maxillary structures of *Hermetia mucens*.

Fig. 18. Mouth structures of *Polistes metricus*. 18ª, ligula, paraglossa and mouth opening; 18ᵇ, labium as a whole, with epipharynx attached; 18ᶜ, maxilla.

Fig. 19. Maxilla of Olfersia. 19ª, seen from front; 19ᵇ, seen from behind or below.

Plate III.

Fig. 1. Mouth structures of Asilidæ—*Laphria* sp. *a*, maxilla from front ; *b*, same from behind , *c*, labium ; *d*, labrum ; *e*, transverse section of mouth at junction of galea and subgalea.

Fig. 2. Mouth structures of *Ramphomyia longicauda*. *a*, the labium ; *b*, maxilla ; *c*, extension of front of head ; *d*, relation of this extension to the labium.

Fig. 3. Galea of an *Andrena* allied to *virina*.

Fig. 4. Mouth parts of *Bittacus strigosus*. *a*, mandibles and labrum ; *b*, maxilla and labium ; *c*, mandibles and labrum—epipharynx of *Panorpa rufescens*.

Fig. 5. Labial structures of *Eristalis tenax*. 5^a, transverse section at about middle ; 5^b, same at about tip.

Fig. 6. Labial structure of *Bombus* sp. 6^a, transection at about middle ; 6^b, same made near tip.

Fig. 7. Labium of *Harpalus caliginosus*.

Fig. 8. Maxilla of *Periplaneta orientalis*.

Fig. 9. Maxilla of Perlid larva.

Fig. 10. Epipharynx of *Eristalis tenax*.

Fig. 11. Mouth parts of *Bibio* sp. *a*, maxilla from behind ; *b*, same in front ; *c*, transection made near the base.

Fig. 12. Labium of *Bombus fervidus* ; the transections are lined to the portions referred to.

Fig. 13. Labium of *Chrysops vittatus* ; the transections are lined to the parts referred to.

Fig. 14. Labium of *Hermetia mucens*.

Fig. 15. Maxillæ and labium of *Bombus*, showing the relation of the parts to each other.

Fig. 16. Maxilla of *Sialis*.

Fig. 17. Maxilla of *Hydrophilus* from upper and lower surface, redrawn from Comstock.

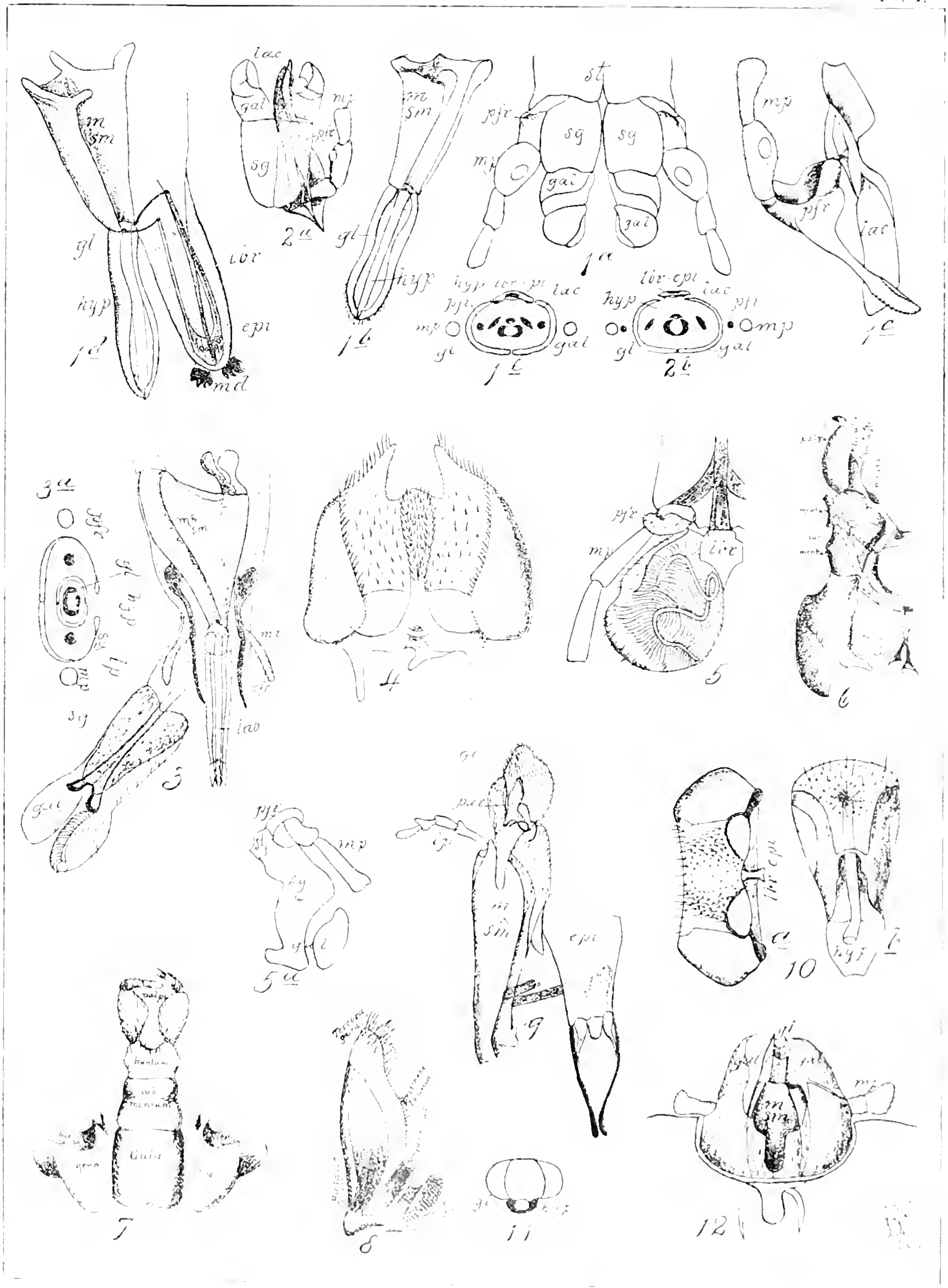
Fig. 18. Maxilla and labium of *Pteromalus*, redrawn from Ashmead.

Fig. 19. Maxilla of *Pronuba*, male.

Fig. 20. Maxilla of *Nemognatha*.

Fig. 21. Maxilla of *Pronuba*, female.

Fig. 22. Mouth parts of *Locusta* from Kolbe. *i*, labrum ; *ii*, mandibles ; *iii*, maxillæ ; *iv*, labium.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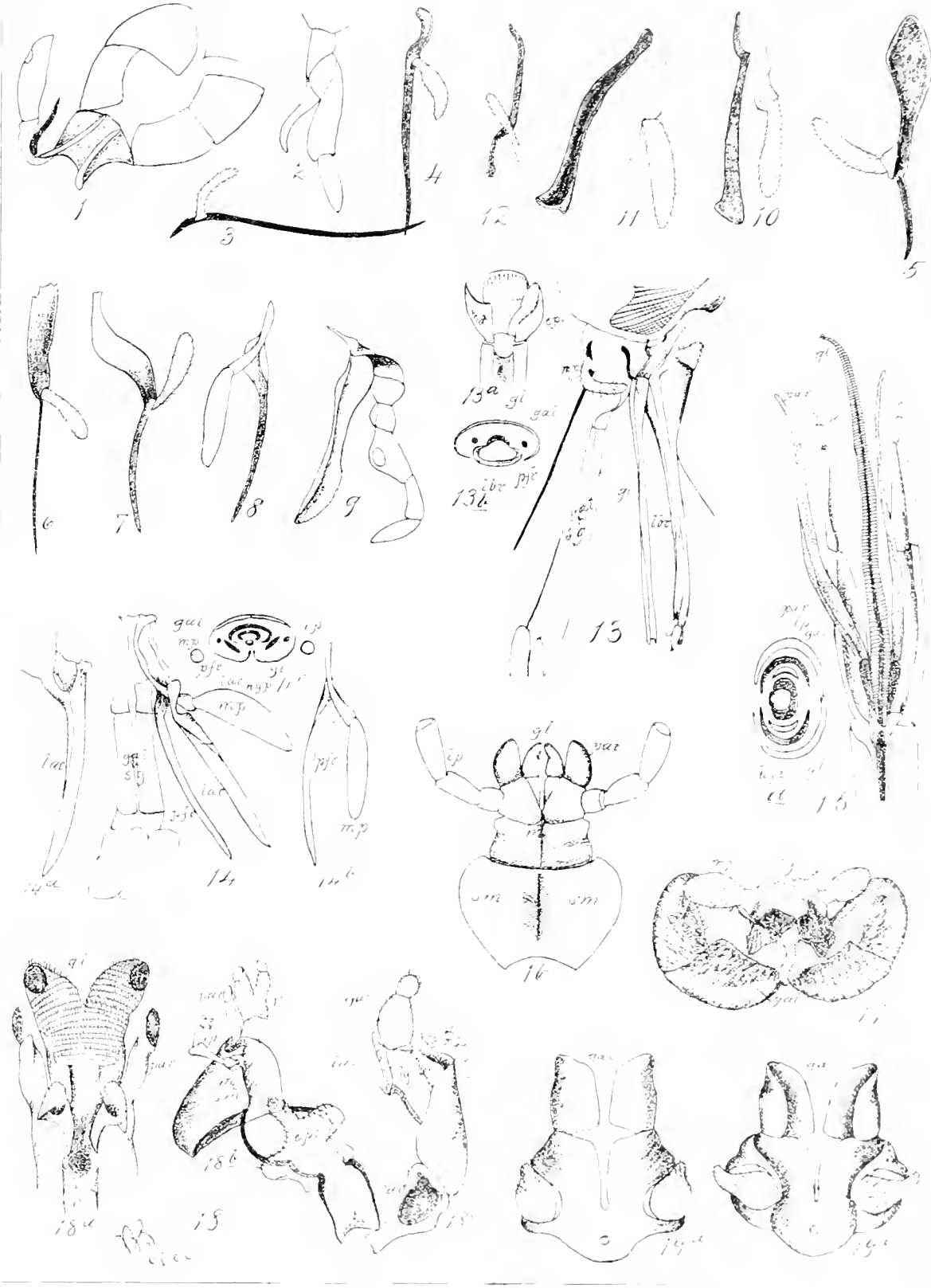
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